STUDIES ON THE PHYSIOLOGY OF REPRODUCTION IN THE DOMESTIC FOWL. XVI. DOUBLE EGGS.[1]

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Among the eggs of the domestic fowl an egg which contains another egg is quite rare, but one or more such specimens have been observed by most persons who have handled large numbers of eggs. This phenomenon has excited the interest of poultrymen and scientists and a number of specimens have been described in the agricultural and scientific literature. The purpose of the present paper is to describe several specimens observed at the Maine Agricultural Experiment Station which have been laid or have been found partly formed within the oviduct at autopsy and to discuss the formation of these abnormalities from the physiological point of view.

Parker (12) published an extensive bibliography on the subject and discussed at some length the recorded cases in connection with four cases which he had himself observed. Von Durski (6) also cites a number of other cases collected from the literature and gives a bibliography. Summarizing these cases briefly we arrive at the following conclusions:

1. Either a normal egg or a dwarf egg which contains little or no yolk may be enclosed with a normal yolk in a second set of normal egg envelopes. The included egg may lie near the yolk of the including egg or it may be enclosed only in the outer layers of albumen.

2. Either a normal or a dwarf egg may be enclosed in a set of normal egg envelopes without any yolk being present in the enclosing egg.

3. When the included egg has a blunt and a pointed end which are distinguishable, it always lies with its pointed end toward the pointed end of the including egg.

[1] Papers from the Biological Laboratory of the Maine Agricultural Experiment Station No. 97.

4. When a yolk is present in the including egg it always lies toward the blunt end, while the included egg occupies the pointed end.

These facts indicate that a normal or a dwarf egg which has passed through the duct as far as the isthmus (when the included egg is only membrane covered) or shell gland (when it has a hard shell) may be returned up the duct without reversing the poles of its long axis. Somewhere, usually in the albumen region,[1] the direction may again be reversed. If the succeeding egg is already forming in the duct the egg which has been forced back lies in the duct posterior to this. As the forming egg completes itself enclosing its predecessor the enclosed egg will of necessity lie in the pointed end and the extent that it is imbedded within the albumen of the enclosing egg will depend on the level of the duct where the two eggs unite. If there is no second egg in the duct the egg which has been returned may stimulate the duct to the secretion of the egg envelopes.

The sixteen double, or enclosed eggs which we have had the opportunity of examining include specimens which show many interesting peculiarities. They will, therefore, be described individually. They may, however, be classified according to their general structure into (1) double eggs with the enclosing egg a normal egg and (*a*) the enclosed egg also normal, or (*b*) the enclosed egg a dwarf egg; and (2) double eggs in which the enclosing egg does not contain a yolk but is simply a set of egg envelopes enclosing (*a*) a normal egg, or (*b*) a dwarf egg.

I. Double Eggs in Which the Enclosing Egg is a Normal Egg.

This group includes specimens 1 to 5.

(*a*) *The Enclosed Egg is Also a Normal Egg in Specimens 1 and 2.*

Specimen 1 (Plate I) was produced at the Maine Station poultry plant. The external appearance of this egg was that of a large membranous sac distinctly pointed. At the blunt end

[1] Gruvel (7) describes a case where the included egg lies between the egg membranes of the including egg indicating that the returned egg came upon its successor in the isthmus instead of within the albumen region, as in all the other cases known to the author.

the sac was continued into a stalk about the size of the index finger. The sac and appendage were covered with a very thin layer of shell. The membrane was ruptured at the foot of the stalk, exposing a large area of the shell of the normal egg which was included. The torn edges of membrane were stuck tight to the shell of the included egg apparently by the thin layer of shell which covered the membrane. There were also folds in the membrane at the foot of the stalk and the inner parts of these folds were not covered with shell. Apparently this rupture and folding of the membrane took place before the shell on the enclosing egg was formed. It will be noted that the enclosed egg lies entirely to one side with its pointed end toward the pointed end of the enclosing egg. At the pointed end of the enclosing egg there is a fresh rupture. From this albumen and yolk were protruding when the egg was found. The yolk had been broken but appeared to have been a normal yolk. The stalk was still filled with albumen. Evidently this rupture had occurred when the egg was laid and was no doubt due to the large size of the egg. The enclosed egg was normal in all respects. Apparently this normal egg had been forced back up the oviduct without reversing its polarity. It apparently met the succeeding egg at the posterior end of the albumen secreting region since it evidently lay quite outside the albumen of this egg. The shape of the enclosing egg indicates that the two eggs passed through the isthmus side by side. There was no membrane around the enclosed egg. That is it did not receive a membrane when it passed up the duct.

Specimen 2 (Plate II. and Figs. 1 and 2) was presented to the Station by Mrs. Ethel Pike, of Winthrop, Maine. Several days elapsed after the egg was laid before it reached the Station laboratory. The egg was well protected but some evaporation had evidently occurred as there were folds in the enclosing membrane which was without shell. Within this membrane lay two normal eggs with their long axes parallel. One of these was a normal egg enclosed in an egg membrane and shell. The other was a normal yolk enclosed in a normal albumen envelope. There was a shallow layer of thin albumen common to the two eggs. It will be seen in the photograph that the folds in the

enclosing membrane were all in the part which covered the naked egg as the shell of the included egg maintained the shape of that part of the outer membrane which covered it. As in the case of specimen number 1, the normal egg was evidently returned up the duct meeting the succeeding egg in the lower part of the albumen secreting region. The two then passed back through the isthmus, with their long axes parallel to each other. Whether or not they were also parallel to the long axis of the duct is impossible to tell since the complete egg was not pointed. In this case also there was no membrane surrounding the shell of the enclosed egg. That is, it did not receive a membrane as it passed up through the isthmus.

(*b*) *The Enclosed Egg was a Dwarf Egg in Specimens 3, 4, and 5.*

Specimen 3 was produced at the Maine Station poultry plant. It had the external appearance of a double-yolked egg with normal shell membranes and shell. The dimensions of this egg were: length 72.1 mm., breadth 46.0 mm., and weight 82.0 gm. On opening the egg it was found to contain at its blunt end a normal yolk which weighed 18.06 gm. and at its pointed end a small spherical soft-shelled dwarf egg which weighed 13.07 gm. A photograph of the contents of this egg is shown in Plate III.,

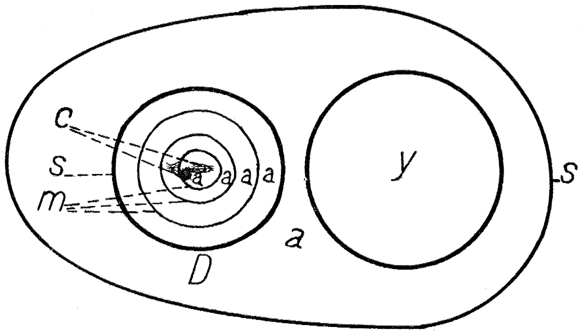

FIG. 1. Diagrammatic sketch showing the structure of double egg No. 3. D = dwarf egg composed of four concentric dwarf eggs; Y = normal yolk; a = albumen; c = chalazal-like fibers; m = egg membrane; s = shell.

Fig. 1, and a diagrammatic sketch of its structure is shown in Text-figure 1.

The dwarf egg lay in the pointed end and the yolk in the

blunt end of the enclosing egg. The fact that the dwarf egg is enclosed in only the outer thick albumen layers may readily be seen from the photograph. No chalazæ were visible in the enclosing egg. The structure of the dwarf egg was quite complex. It consisted of a series of four concentric egg membranes separated from each other by layers of clear thick albumen. Within the inner membrane was a mass of chalazal-like coagulation fibers surrounded by thick albumen. Attached to one end of the innermost egg was a mass of coagulation fibers. There was no shell on any of the egg membranes except the outer one. The structure of this egg indicates that a very small dwarf egg passed back from the isthmus to the albumen-secreting region, acquiring some chalazal fibers and a small amount of albumen. It then passed into the isthmus, received another membrane, and was then returned to the albumen-secreting region, where it received another albumen layer. Passing again to the isthmus it received its third membrane. It was again returned to the albumen region where it received another layer of albumen. It then passed through the isthmus into the shell gland receiving an egg membrane and a thin layer of shell. It was then returned again to the lower portion of the albumen-secreting region where it met a normal yolk surrounded by several layers of albumen and became enclosed with this in a few layers of albumen and egg membrane and shell. The fact that the albumen separating the concentric egg membranes of the enclosed dwarf egg was in each case the clear thick albumen, secreted so far as is known only in the albumen secreting region, compels the conclusion that the egg passed from isthmus to albumen-secreting region several times. This indicates a considerable disturbance of the normal movements. Whatever the nature of this disturbance the egg record of the bird shows that it was of temporary character, since the bird had been producing and continued to produce normal eggs in regular series. The double egg was the first egg of a two egg clutch. It followed a four-day non-production period, on the last day of which the bird nested but did not lay.

Specimen 4 was brought to the Maine Station biological laboratory by Dr. O. A. Johannsen. The egg had been broken

for domestic use, so that its internal arrangement could not be certainly ascertained. It was of a practically normal size and contained a normal yolk and a very small dwarf egg which weighed 4 gm. This dwarf egg contained a small piece of hardened secretion about the size of a pinhead surrounded by layers of albumen which were distinctly visible by transmitted light. The membrane of the dwarf egg was quite thick and the shell very thin. After a short stay in the shell gland the dwarf egg had apparently been returned to the albumen-secreting region without receiving a membrane on its upward passage. Here it met and became enclosed in the succeeding egg.

Specimen 5 was brought to this laboratory by Mr. H. W. Smith. This egg had been broken for laboratory purposes. He said that the egg was of normal external appearance and average size. He did not note the relation of the internal structures to the poles of the egg. The egg contained a normal yolk. Separated from this by a few layers of thick albumen was a worm-like membrane-covered dwarf egg. This dwarf egg

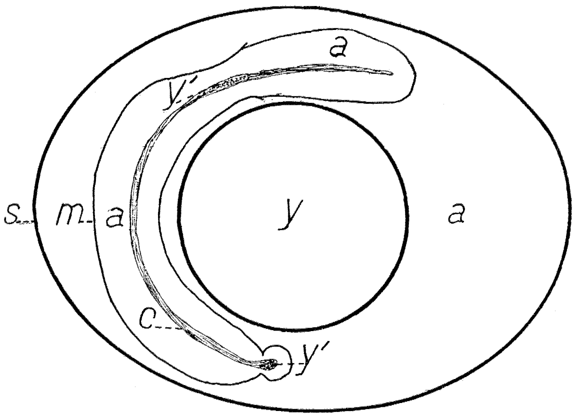

FIG. 2. Diagram showing structure of dwarf eggs No. 5. a = albumen; c = chalazal-like fibers, m = egg membrane; s = shell; y = normal yolk; y' = yolk droplets.

was bent around the yolk. The yolk and dwarf egg were included in a common albumen envelope. The structure of this egg is shown in Fig. 2. The resemblance of the dwarf egg to a simple organism of some kind was striking. Running through

the middle was a string of coagulation fibers like untwisted chalazal threads. Mixed with these at certain points were small droplets of yolk. The membrane covering the dwarf egg was complete at one end and open at the other. The albumen surrounding the chalazal-like core was thick. The chalazal core surrounded by thick albumen continued beyond the membrane at the open end. This naked portion separated definitely from the surrounding albumen when the dwarf egg was taken from the albumen. Evidently this cylindrical dwarf egg had passed partly into the isthmus and had then been returned into the albumen region where it became enclosed in the succeeding egg.

II. Double Eggs in Which the Enclosing Egg is a Set of Egg Envelopes with no Apparent Nucleus Except the Enclosed Egg.

(*a*) *The Enclosed Egg was a Normal Egg or at Least Had a Normal Yolk in Specimens 6, 7, 8, 9 and 10.*

Specimen 6 was laid by a normal bird belonging to the Maine Station flock. In external appearance it resembled a large hard-

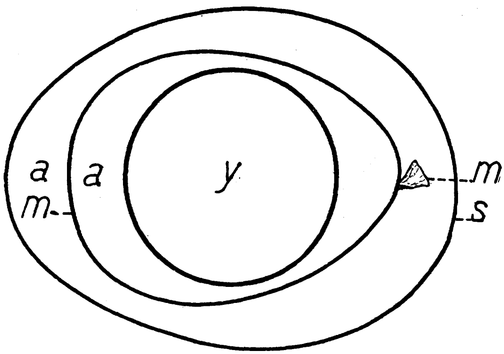

FIG. 3. Diagram showing the structure of double egg No. 6. *a* = albumen; *m* = membrane; *s* = shell, *y* = normal yolk.

shelled double-yolked egg. A diagram showing the structure of this egg is shown in Fig. 3. The entire egg weighed 94.74 gm. When the egg was opened it was found to contain a membrane-covered egg surrounded by a layer of thick and a layer of thin albumen. This albumen weighed 57.39 gm. The weight of

the shell was 8 gm. The enclosed egg weighed 29.36 gm. Attached to one pole of the enclosed egg by the inner layer of thick albumen was a white mass which on close examination appeared to be a triangular piece of egg membrane. The enclosed egg was membrane-covered. Its contents resembled a large normal egg as it appears while it is in the upper part of the albumen-secreting region of the oviduct. That is, it consisted of a large yolk (weight 23.16 gm.) surrounded by a thin layer of very thick clear albumen which adhered closely to the yolk. This albumen weighed only 5.57 gm. The enclosed egg was distinctly pointed and lay with its pointed end toward the blunt end of the enclosing egg. It has been noted that in all the cases described and reviewed by Parker (12) when a pointed end was distinguishable in both included and including eggs the pointed end of the former always lay toward the pointed end of the latter. In this particular, therefore, the above described case differs from those known to Parker. Since specimen No. 7

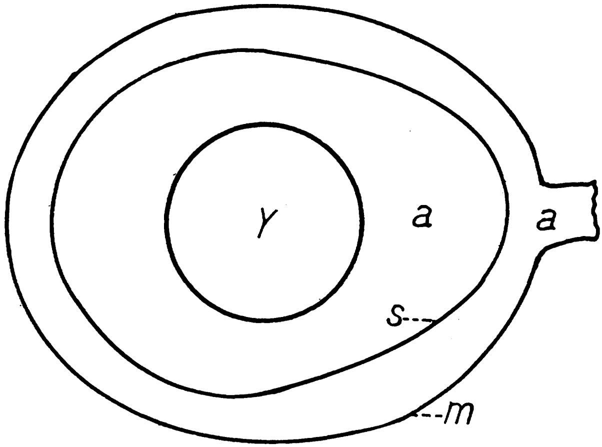

FIG. 4. Diagram showing the structure of double egg No. 7. *a* = albumen; *m* = egg membrane; *s* = shell; *y* = normal yolk.

also shows the poles of the included egg in the reverse direction to those of the including egg, this case will be described and the reversal of axes will then be discussed.

Specimen No. 7 was brought to this laboratory by Dr. W. J. Morse. This egg was a large membrane-covered egg with a short tubular attachment. A diagram showing its structure is given

in Fig. 4. It contained a normal hard-shelled egg surrounded by a thin layer of albumen[1] which extended into the stalk. The pointed end of the included egg lay toward the stalked end of the including egg. The including egg did not show a perceptible pointing of the end opposite the stalk but several distinctly pointed stalked eggs have been observed at this laboratory. In all cases the stalk occurred at the blunt or air cell end of the egg. Two stalked and pointed double eggs have occurred (see Plate I. and Text-fig. 5) and in these cases also the stalk was at the blunt end. Further eggs have been found in the oviduct which had not rounded off completely at the end toward the funnel but were trailing a stalk of albumen. In no case has an egg been observed in the duct which was not rounded off at the end which was toward the caudal end of the duct. A few words in regard to the processes involved in shaping the egg seem necessary at this point.

Before the egg receives its egg membrane it is a fluid body which tends to take a spherical form. It becomes elongated in the direction of the long axis of the oviduct due to the fact that the diameter of the oviduct is smaller than the diameter of the egg if it maintained a spherical form. The outline of an egg is sometimes nearly elliptical indicating that the duct did not offer much resistance to the egg when the peristaltic action of the duct walls forced it forward. More often, however, one end of the egg is distinctly more pointed than the other. This distinction between the two ends is seen in many of the membrane-covered eggs found in the isthmus at autopsy. It seems probable that the relative tension of the longitudinal and circular fibers of the duct wall at the time the egg receives its membrane is the most important factor in determining the shape of the egg. If the longitudinal fibers in the wall of the duct ahead of the egg do not contract enough considerably to enlarge the duct as the contraction of the circular fibers behind forces it forward, the egg will meet with considerable resistance and will tend to become pointed. In all cases observed where an egg in the isthmus had its poles differentiated the pointed

[1] As the egg had been preserved in 70 per cent. alcohol, the albumen was coagulated and its normal consistency could not be observed.

end of the egg lay toward the caudal end of the duct. So far as we know if an egg becomes pointed the pointed end is always the end away from the funnel end of the oviduct. For convenience we may speak of the end which first passed down the duct as the anterior end and the opposite end as the posterior end of the egg. In an egg which is distinctly pointed the anterior end is the pointed end and the blunt end is the posterior end. From the facts cited in the preceding paragraph it is practically certain that the presence of a stalk attached to one end of an egg also differentiates the poles, the stalked end being the posterior end.

In specimens 6 and 7 the anterior and posterior end of both included and including eggs were differentiated. Both included and including egg of specimen 6 were pointed. The including egg of specimen 7 was stalked. In both 6 and 7 the anterior (pointed) end of the included egg lay toward the posterior (blunt or stalked) end of the including egg. Parker pointed out that the location of the pointed end of the included egg at the pointed end of the including egg indicates that the included egg has been forced up the duct without reversing its poles. Patterson (13) describes a double egg in which the long axis of the enclosed egg meets the long axis of the enclosing egg at an oblique angle. "On account of this inclination of the enclosed egg its pointed end lies nearer to the blunt than to the pointed end of the enclosing egg." In regard to the significance of this unusual orientation Patterson says "This unusual position of the enclosed egg doubtless has been brought about by crowding and does not indicate necessarily that it was at first incorrectly oriented." However, the observance of cases 6 and 7, where the anterior end of the enclosed egg lies toward the posterior end of the enclosing egg, indicates that the reversal of the poles of the enclosed egg sometimes occurs. The small diameter of the oviduct when compared to the length of the long axis of the egg raises the question, How can this reversal take place?

It has been stated that when a pointed egg was found in the isthmus in all observed cases the pointed end was caudad. This position in reference to the axes of the duct was also maintained by a large per cent. of the eggs which have been found in the

shell gland at autopsy or have been found partly extruded from the cloaca in cases of egg-bound birds. However, we have observed a few cases where the egg in the shell gland or partly extruded was blunt end caudad. Moreover, a series of observations carried on at this laboratory confirm Bonnet's (1) statement that the pointed end of the egg is usually laid first but that occasionally the blunt end comes out first.

Since so far as we know the egg is always formed with its pointed end caudad but is sometimes laid blunt end first it seems probable that in the latter cases the egg turns in the duct. In this connection the results of some rough preliminary experiments in an investigation of the mechanism of laying are of interest. During routine autopsy work hard-shelled eggs found in the shell gland were forced out by pressure from behind. Usually the eggs passed directly backward and out pointed end

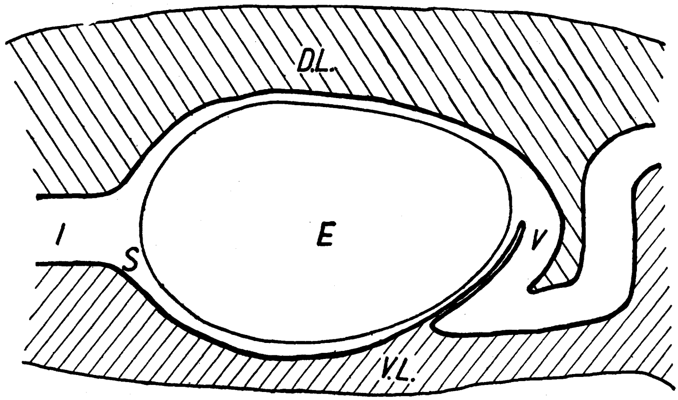

FIG. 5. Diagram showing an egg in the shell gland. *D.L.* = Dorsal ligament; *E* = egg; *I* = isthmus; *S* = shell gland; *V* = vagina; *V.L.* = ventral ligament.

first, but several times the pointed end turned dorsad and the egg reversed ends. Continued pressure then forced the egg out blunt end first. Fig. 5 shows a diagram of the egg in the uterus.

If pressure is so applied that the pointed end is pressed directly into the opening of the vagina or ventral to it on the thin fold the egg comes out pointed end first. However, if it is pressed against the uterine wall slightly dorsal to the vaginal opening, the point slips along this curved caudodorsal angle of the uterus

and the egg reverses ends. In the region of the uterus the ventral ligament becomes a thick band of muscle fibers from which fibers extend over the uterus, some of them reaching the caudo-dorsal angle of the body wall. This band of muscles is no doubt an important, perhaps the chief mechanism concerned in extruding the egg. Since it is heaviest on the ventral side of the uterus and since fibers connect it to the body wall dorsal to the opening of the vagina, it seems reasonable that their contraction in normal laying may sometimes bring the point of the egg against the uterine wall dorsal to the opening of the vagina and that in such a case the egg reverses ends.

In cases 6 and 7 the reversal of the axes of the included egg may have occurred in this manner and then a change in direction of the muscular action of the duct may have forced the egg back up the duct pointed end first. In the albumen-secreting region the direction was again reversed. In each of these cases the included egg appeared to be the only nucleus of the including egg and it seems probable that it furnished the necessary stimulus to cause the secretion of the including egg envelopes. There was no membrane immediately surrounding the included egg. Evidently it did not acquire one going up.

Specimens 8 and 9 were found in oviducts during routine autopsy work. They show the processes of double egg formation in actual operation. Specimen 8 was found in the albumen-secreting region with its posterior end 10 centimeters from the beginning of the isthmus. The included egg was surrounded by a layer about one half cm. deep of very thick albumen. Underneath this was a firm egg membrane within which was a normal hard-shelled egg surrounded by a layer of thick and one of thin albumen. Evidently this egg had been forced from the uterus up the duct to the albumen-secreting region. Since there was no membrane around the egg inside the albumen envelopes it could not have received a membrane going up. In the albumen-secreting region its direction was again reversed and it evidently stimulated the secretion of albumen and egg membrane. It was then again returned into the albumen-secreting region where it again stimulated the secretion of albumen. In this condition it was found at autopsy.

Specimen 9 was found with the craniad or blunt end of the included egg 14 centimeters from the funnel mouth. The normal hard-shelled egg had a shell membrane around the shell. There was no albumen between the shell and this membrane. Either the egg had received this membrane on its way up or it had been carried into the albumen-secreting region and immediately carried back into this isthmus and after receiving the membrane had been carried back up the duct nearly to the funnel mouth. This had probably happened only a short time before death, since there was no albumen formed around the outer shell membrane.

A diagram of specimen 10 is shown in Fig. 6. From the

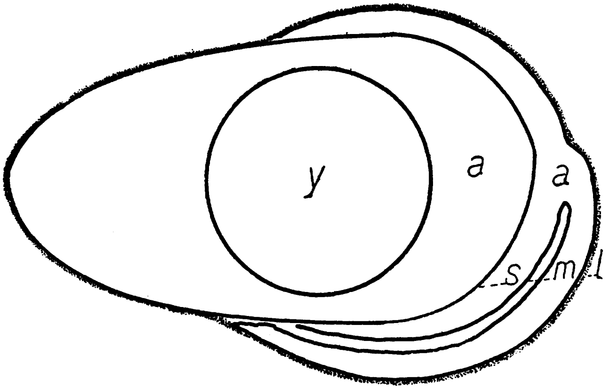

FIG. 6. Showing the structure of double egg No. 10. a = albumen; l = granular shell material; m = egg membrane; s = shell; y = normal yolk.

figures it may be seen that the enclosed hard-shelled normal egg is not entirely surrounded by all of the envelopes of the enclosing egg, but the second egg membrane filled with albumen forms a cap which covers the blunt half of the enclosed egg. At the posterior pole of the egg the enclosing cap of egg membrane is continued into a stalk also filled with albumen. This stalk is folded down against the side of the egg. The whole egg is covered with a continuous layer of granular shell material. The stalk of the including egg must have been folded down before this shell was secreted as the under side of the stalk and the part of the egg membrane against which it lay were free from shell.

In this case also it is apparent that a normal distinctly pointed hard-shelled egg was forced back up the duct without reversing its poles. The question of where the direction was again reversed is less easily decided. The fact that the pointed half is not covered with membrane suggests that it was forced only half way into the isthmus, this would not account for the presence of thick albumen in the cap and stalk. While Pearl and Curtis (13) have shown that albumen is secreted in the isthmus and uterus, they have seen no evidence of as thick gelatinous an albumen as that found in this egg outside of the albumen-secreting region. It would seem that the egg had been forced back part way into the albumen-secreting region and had either stimulated the formation of albumen or had met a stalked dwarf egg coming down. Why in this case membrane was not formed around the whole enclosed egg is difficult to say. While it is possible that some albumen is necessary to cause the secretion of an egg membrane, case 9 above and two cases described in an earlier paper (4) have shown an egg membrane closely applied to a hard-shelled or a membrane-covered egg with no visible albumen between them.

Another peculiarity of this egg is the position of the stalk. Stalked eggs while infrequent are a well-known type of abnormal eggs. The stalk is usually continued straight in the long axis of the egg. Sometimes it is more or less coiled or crushed down onto the blunt pole of the egg and sometimes in this position it becomes covered with shell and forms a projection more or less resembling a snail shell. How pressure from behind could cause the straight folding down seen in specimen 10 is hard to imagine. If the egg immediately on entering the uterus had its poles reversed in the manner described on page 191 this position of the stalk would be the natural result. If this is the explanation, the reversal of poles must have occurred before the shell was formed. The egg must then have remained in the uterus for some time before it was laid.

(*b*) *The Enclosed Egg Was a Dwarf Egg in Specimens 11, 12, 13, 14, 15 and 16.*

Specimen 11 was a soft-shelled dwarf egg which weighed 11.1 grams. When this egg was opened it was found to contain a

small hard-shelled dwarf egg surrounded by very thick albumen. This small egg had a short stalk which was open at the end. The enclosed egg including the stalk was filled with a clear thick albumen. The stalked end of the enclosed egg lay toward the blunt end of the enclosing egg. Evidently this short-stalked dwarf egg had been returned from the shell gland to the albumen-secreting region without reversing its poles and without acquiring an egg membrane going up. It had then evidently furnished the stimulus for the formation of the enclosing envelopes.

A photograph of specimen 12 is shown in Plate III., Fig. 2. This egg was much like specimen 11, but was much larger. The complete egg weighed 32.0 grams. Both enclosed and enclosing eggs had hard shells. The enclosed egg contained a mass of chalazal fibers surrounded by rather thin albumen. One end of this egg was contracted to a short stalk-like portion. There was a circular area at one side of the end of this stalk-like appendage which was not covered with either membrane or shell. That is, the albumen was exposed. The enclosed egg weighed 7 grams. Externally it was lightly covered with a mass of chalazal-like fibers which projected from the poles into the albumen. In the mass at the finished end was a small drop of yolk and a small lump of hardened albumen. Surrounding the central mass formed by the dwarf egg, yolk drop and lump of hardened albumen with their wrapping of chalazal-like threads were layers of thick and thin albumen. The unfinished end of the included egg lay toward the blunt end of the including egg. Evidently without turning around the enclosed egg had backed up the duct nearly to the funnel mouth. It had not acquired an egg membrane going up. It had there united with the drop of yolk and the lump of hardened albumen. Either these particles or the included egg, or both together, had furnished the stimulus for the secretion of the egg parts of the including egg.

Specimens 13, 14 and 15 are so nearly alike that one description will suffice for them all. These eggs varied in weight from 12.5 to 15.0 grams. Each egg was hard-shelled. A diagram of No. 13 is given in Fig. 7. With slight modifications in the size and shape of the irregular mass of yolk this diagram would represent equally well either of the other two eggs. In each of

these cases the enclosed egg was a membrane-covered egg without any visible distinction between the poles. In each case the enclosed egg contained a small irregular mass of yolk wrapped in a mass of chalazal-like threads and surrounded by albumen. In specimens 13 and 14 all of this albumen was thick, but in specimen 15 both thick and thin albumen were present. In each case the included egg had at each pole a bunch of chalaza-like fibers resembling imperfect chalazæ. In each case the

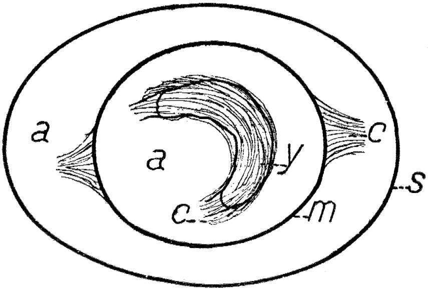

FIG. 7. Diagram showing the structure of double egg No. 13. *a* = albumen; *c* = chalazal-like threads; *m* = egg membrane; *s* = shell; *y* = yolk.

including egg contained both thick and thin albumen. Evidently in each case a dwarf egg which contained a small amount of free yolk was returned from the isthmus to the uppermost part of the oviduct and there furnished the stimulus for the formation of the including egg.

Specimen 16 is somewhat similar to the three eggs just described. In this case the included egg did not contain yolk. Neither were there visible chalazæ at its poles. That is, a yolkless membrane-covered dwarf egg was evidently returned to the albumen-secreting region where it furnished the nucleus for the including egg.

Brief Description of Four Double Eggs Found in the Body Cavity of a Bird with an Abnormal Oviduct.

Beside the 16 specimens described above, 4 specimens were found in the body cavity of a bird with an abnormal oviduct. The case has been described in a previous paper (4). "The oviduct was perfectly normal from the funnel mouth to the posterior end of the isthmus where the tube ended blindly.

There was no shell gland or vagina." This bird had a normal ovary and the oviduct functioned as far as it was developed. The eggs were then backed up the duct into the body cavity where they were absorbed. A large number of empty egg membranes and 14 eggs in every stage of absorption from a normal fresh membrane-shelled egg to empty egg membranes were found in the body cavity at autopsy. While most of these eggs had apparently been normal, 4 of them were double eggs. In one of the four the enclosed egg was also a double egg. Another one was made up of a concentric series of four enclosed eggs. A brief description of these four eggs is given in the original paper.

Discussion.

The occurrence of double eggs is not infrequently noted in the agricultural journals. Such eggs have usually been mistaken for normal or double-yolked eggs until broken for domestic use. The observations on the arrangement of the contents is, therefore, usually not noted. When descriptions of the arrangement were attempted they have for the most part agreed with those described above. E. W. Pick (11), however, describes a double egg in which he states that the normal yolk was in the "tapered or smaller end of the egg, while in the 'bell' or larger end there nestled a smaller egg, shell intact." So far as we know in all other cases observed where an egg is enclosed in another egg which contains a yolk the yolk is in the blunt or bell end. The egg described by Mr. Pick was supposed to be "an ordinary double-yolked egg" until "broken for domestic use." Since it is necessary to observe very carefully the arrangement of the parts of an egg before they are taken from the shell in order to be sure the positions have not been disturbed it seems possible that in this case the record may not be accurate. In specimens 1 and 2, however, a common egg membrane enclosed a normal hard-shelled egg and a naked egg composed of a normal yolk surrounded by albumen. These two eggs lay with their long axes parallel. At least in specimen 1 the evidence is convincing that the two eggs passed through the isthmus side by side. If two eggs can come side by side as in these cases it is at least possible to conceive that they may occasionally pass. In such a

case the reversal of the direction of the upward moving of the hard-shelled egg after it had met and passed its successor might result in a double egg with a yolk in the pointed end and a hard-shelled egg in the blunt end.

Parker (12) cites cases of "soft-shelled" eggs in the body cavity described by Davaine (5) and Landois (10). Several other cases are described by von Durski (6). A few cases of membrane-covered or normal hard-shelled eggs in the body cavity of apparently normal birds have been observed by the authors. A previous description (3) of a bird which backed all her eggs into the body cavity due to the fact that the oviduct ended blindly at the posterior end of the isthmus has been briefly summarized on page 196. It has also been shown by Pearl and Curtis (15) that eggs are found in the body cavities of birds killed some months after their oviducts have been ligated in the isthmus or shell gland. If the ligature is in the isthmus the eggs are membrane-covered but if all or part of the shell gland lies above the ligature some or all of the eggs have shells. Since the egg membrane and shell are formed in the caudal portion of the oviduct and since in all the above cases where eggs were found in the body cavity the funnel mouth was the only opening of the oviduct into the body cavity, the egg must have been returned up the duct and out through the funnel mouth after having passed as far as the isthmus or shell gland. In two cases the authors have observed hard-shelled eggs with no secretion around them in the upper portion of the albumen-secreting region. Specimens No. 8 and 9 described above were also hard-shelled eggs found in the albumen-secreting region of the duct. In these four cases also the eggs must have been returned from the shell gland.

So far as we know an egg has never been observed moving up the duct nor have any movements of the duct been observed which would tend to force an egg in that direction. It has been generally assumed (Parker 12, von Durski, 6, Hargitt 8, Patterson 13, and Pearl and Curtis 15) that the backward movement of the egg is due to antiperistalsis. In the present paper no assumption has been made as to the nature of the muscular action. It seems possible that this may take some other form

than antiperistalsis. C. J. Hick and J. W. Visher (9) have lately analyzed the muscular movements which cause regurgitation of the duodenal contents into the stomach and have found that they are not antiperistaltic in character. The precise nature of the movements of the oviduct which force an egg backward can be more safely decided after they have been observed or experimentally produced. An examination of the cases discussed in the literature and described above give little evidence that the oviduct glands are excited to pour out their secretion by an egg moving up the duct. If this were the case a complete normal egg in the body cavity or in the upper part of the oviduct or included within another egg would have a reversed set of egg envelopes surrounding the shell. That is, around the shell would be an egg membrane. This membrane might be separated from the shell by thin albumen since it has been shown (14) that this albumen is formed in the isthmus and uterus and taken into the egg through the egg membrane probably by osmosis. Whether or not thin albumen can come in after the thick albumen is covered by a completed shell is not known. The egg normally comes to its full weight before the shell is very thick. Surrounding the egg membrane we would then find a layer of thick albumen. This is not the case in most eggs which have backed up the duct. The eggs found in the body cavity and upper oviduct as a rule were in the same condition as an egg from the lower part of the duct. In case they were included or were becoming included in a second set of egg envelopes these envelopes were in the same oder in the including as in the included egg. That is, albumen, egg membrane and shell. This indicates that the envelopes were formed during a second passage down the duct. In this connection Hargatt (8) says: "If it should be queried why such deposition might not have taken place on the ascent of the egg by antiperistalsis as well as during its later descent, it may suffice to admit that perhaps it did occur. However, in case the return of the egg up the oviduct took place soon after its original descent, the glandular structure would be in a state of exhaustion and hence capable of only slight discharge." However, it has been shown in earlier investigations from this laboratory (2) that the passage

of a normal egg does not exhaust even temporarily the oviduct glands since both albumen and shell are heavier in double-yolked than in single-yolked eggs, while both parts are still heavier in triple-yolked than in double-yolked eggs. It was further shown (3) that in many cases the second yolk must have followed the first quite closely since a normal egg was produced on the day preceding the day on which the multiple-yolked egg was laid. The time between the passage of these yolks must have been less than the time required to form a complete hard shell. The very plausible explanation offered by Hargitt does not, therefore, seem tenable. Two other suggestions may be made but neither of them can be proven at present. One is that perhaps the oviduct is polarized to such an extent that secretion is discharged only when the stimulus advances in the normal direction. The other is that perhaps the egg moves very rapidly up the duct and that there is not sufficient time for the stimulus to become effective. That the egg does move rapidly up the duct is suggested by the fact that in the birds with ducts ligated in the shell gland the eggs with complete shells are forced up the ducts before the succeeding yolks enter the funnels. Normally ovulation takes place very soon after laying.

It should, however, be stated that there are a few cases known where some portion of the duct has for some reason failed to form its normal secretion around an egg which has passed in the normal direction. The two cases which have come under our personal observation may be briefly cited. A photograph of the egg produced in the first case is shown in Plate III., Fig. 3. When the egg was found in the nest the two parts were pressed together over the dark areas which face each other in the photograph. They were held together only by the thin layer of shell which covers all of the two egg membranes except the approximated portions. This shell cracked off when the egg was handled and the circular areas free from shell were exposed. The two eggs had apparently been flattened together but the membrane rounded up as they separated. The egg shown at the right was a normal egg with normal yolk, albumen and egg membrane. The other egg was a normal yolk surrounded by an egg membrane. This egg contained no visible albumen. When

the egg membrane was cut and stripped off the clean normal vitelline membrane was exposed. This egg must have passed through the albumen region of the duct without receiving any perceptible quantity of albumen. Whether this was due to exhaustion of the albumen glands or to a rapid passage of the yolk or to some other cause is not known. Evidently under certain conditions the albumen glands do not respond to their normal stimulus even when passing in the normal direction. A failure of the albumen glands is not necessarily accompanied by a failure of the membrane-secreting glands of the isthmus. This egg evidently overtook the normal egg after it had received its egg membrane but before any shell was formed.

In the other case an apparently normal bird laid an egg which consisted of a normal yolk surrounded by albumen but without either membrane or shell. That is, the membrane- and shell-secreting glands failed to respond to their normal stimulus. In this case also the cause for this failure is not known.

In spite of what seems to be a general rule that including egg envelopes are formed only during a downward passage of the egg, three cases are known in which it is possible that the glands of the isthmus may have been stimulated to the secretion of an egg membrane by an egg passing up the duct. Specimen 9 was a hard-shelled egg surrounded immediately by an egg membrane and was found in the upper albumen-secreting region of the oviduct. As previously suggested, this may have received the egg membrane when passing up or it may have been returned from the lower albumen-secreting region to the isthmus and then again been forced up the duct to the position in which it was found. However, it was more than half way up the albumen-secreting region and had not yet received any albumen. Also two of the double eggs found in the body cavity of the bird with the congenitally closed oviduct had an egg membrane closely surrounding the enclosing egg. In either of these cases the enclosed egg may have received the membranes going up or it may have been temporarily moved caudad from the lower albumen region to the isthmus. In either of these cases it is also possible that there had originally been some albumen between the enclosed egg and the enclosing membrane which had been absorbed.

In a previous investigation (3) attention was called to the possibility that under certain conditions the return of an egg up the duct may result in the formation of a double-yolked egg. It seems quite possible that the reversal of the direction of an egg may be more frequent than we have formerly supposed. The result of such a reversal must depend on the state of development of the egg when the backward motion begins, the extent of the backward movement, the rate of fecundity of the individual bird at the time, etc. For example, if an egg which has not yet received its egg membrane is forced backward toward the funnel but not expelled from the duct and then without meeting its successor moves forward again the only result will be an unusually large amount of albumen. If an egg without a membrane which is moved up the duct but not expelled meets its successor and returns with it through the duct, the result will be a double-yolked egg. While it must be admitted that since the succeeding yolk is not usually ovulated for some hours after an egg has received a membrane, yet yolks are certainly sometimes ovulated at considerably shorter intervals. It is also possible that the tone of the oviduct may sometimes be so low that an egg may remain practically stationary for a time. So soon, however, as the egg receives its membrane it can combine with its successor only as a double egg. Either a normal or a dwarf egg may be returned up the duct and may either be expelled from the funnel into the body cavity or at any level of the duct the direction may again be reversed. If the egg becomes united with its successor it becomes enclosed with it in some common envelopes, the number which are common depending on the level of the duct at which the components unite. If it does not meet its successor it becomes a nucleus around which are formed the envelopes which are normally secreted below the point where the forward direction is again resumed. It thus seems that the formation of a double egg does not involve unique processes, but that this phenomenon results from certain combinations of processes, most of which are the normal processes of egg formation. The abnormal factor—the reversal of direction of the egg—when of greater extent results in the expulsion of the egg into the body cavity from which it is

usually absorbed without difficulty. When the reversal of direction is of less extent the result may be a normal egg with a large percentage of albumen or rarely it may be a double-yolked egg.

Summary.

1. A membrane-covered or hard-shelled normal or dwarf egg may be returned up the duct and may either meet its successor and return with it, becoming enclosed in a common set of egg envelopes, or not meeting its successor it may again be forced through the duct stimulating the secretion of a set of egg envelopes around itself.

2. The number of egg envelopes common to the enclosed egg and the yolk of the enclosing egg or the number of egg envelopes which surround the enclosed egg when the enclosing egg has no yolk depends apparently on the level of the duct at which the enclosed egg resumes its normal direction toward the cloaca.

3. The enclosed egg is usually forced up the duct without turning on its axis but occasionally the poles are reversed.

4. A similar reversal of poles sometimes occurs in normal laying and it seems probable that in both cases this turning takes place in the uterus when the first powerful contractions of the uterus brings the outwardly directed end of the egg slightly above the opening from the shell gland into the vagina and tangentially against the curved caudo-dorsal angle of the uterus.

5. The enclosed egg usually precedes its successor through the duct and, therefore, usually lies in the pointed or anterior end of the enclosing egg, while the yolk of the enclosing egg lies in the blunt or posterior end.

6. However, in two known cases where the enclosed egg united with its successor after the latter had received practically all its thick albumen there is evidence that the two eggs came side by side in the duct with their long axis parallel and in one case they certainly passed through the duct side by side with their long axes parallel to each other and also parallel to the long axis of the duct.

7. There has been one case described with the yolk in the pointed and the enclosed egg in the blunt end of the enclosing egg. There is some doubt about the accuracy of this observation but it is possible that two eggs can pass in the duct.

8. A hard-shelled egg uncovered by membrane or albumen is sometimes found in the body cavity or upper oviduct while a hard-shelled egg enclosed within another egg is not usually immediately surrounded by an egg membrane. It would, therefore, seem that the egg does not cause the secretion of egg envelopes around itself on its way up the duct.

9. Since in the case of a double-yolked egg a second yolk closely following the first does stimulate the secretion of the successive envelopes, it does not seem probable that the failure of the duct to form envelopes around the returning egg is due to exhaustion of the glands.

10. The reason for this failure is not known. It may be that the return of the egg is very rapid and that the time of application of the stimulus is too short to be effectual, or there may be a real polarity of the duct so that it responds only to a downwardly directed stimulus.

11. A few cases are known where one or more of the normal egg envelopes have not been formed around an egg advancing in the normal direction (for example, a yolk enclosed by egg membrane and shell but with no albumen, or a laid egg composed only of normal yolk and albumen). The cause for these phenomena are not known. In these cases the movement of the egg may have been abnormally rapid.

12. The occurrence of membrane-covered or hard-shelled eggs in the body cavity, the albumen-secreting region of the oviduct or enclosed within the albumen of another egg shows that an egg may be moved up the duct, but since an egg has never been observed moving in this direction the nature of the motion can only be imagined.

13. The double egg results from a modification of the normal processes of egg formation due chiefly to a reversal in the direction of the egg after it has received its membrane or its membrane and shell. This backward movement must cease before the egg is expelled from the funnel mouth and the movement in the normal direction must be resumed.

14. If the backward movement sets in before the egg receives its membrane but stops before it is expelled from the funnel mouth and if the normal direction is then resumed, the result

will be a normal egg with a large percentage of albumen or in case the returned egg meets its successor, a double-yolked egg.

15. If the backward movement of an egg in any stage does not stop too soon, the partly or fully formed egg will be expelled from the funnel mouth into the body cavity.

16. In case the oviduct is naturally or artificially closed the eggs are regularly expelled by forcing them out the funnel mouth.

17. A double egg then is the result of a combination of normal and abnormal processes which when combined in other proportions result in other abnormal phenomena of egg production.

18. An egg may move backward and forward several times in the duct as is shown by the production of an egg enclosed within a series of concentric egg membranes separated by thick albumen.

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DESCRIPTION OF PLATES.

Plate I.

Photograph of double egg No. 1. See description page 182.

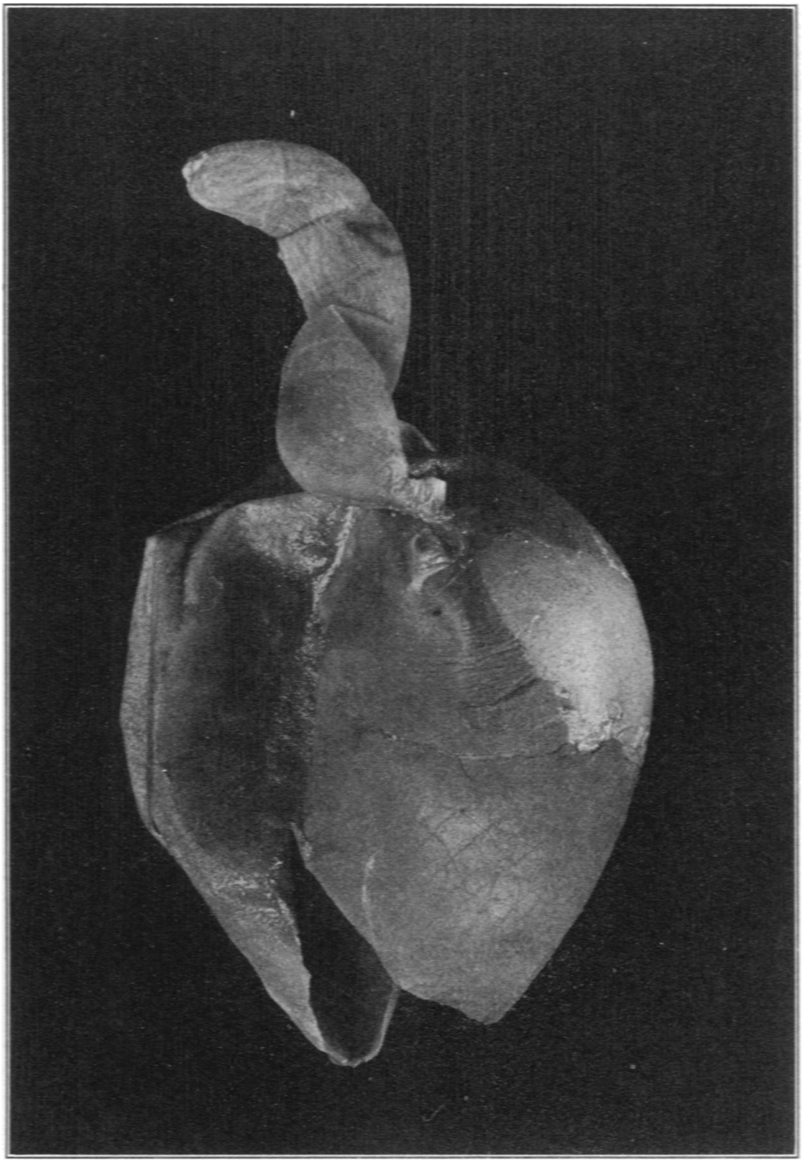

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PLATE II.

Photographs of double egg No. 2. Fig. 1, outside view. Fig. 2, view after. outer membrane was opened.

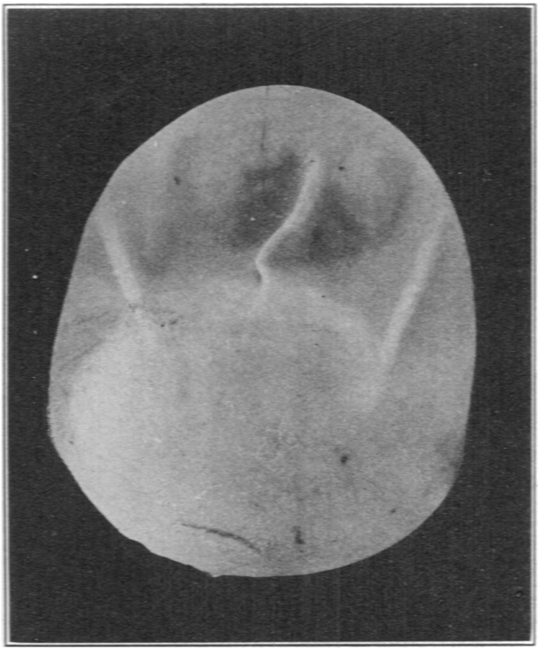

FIG. 1.

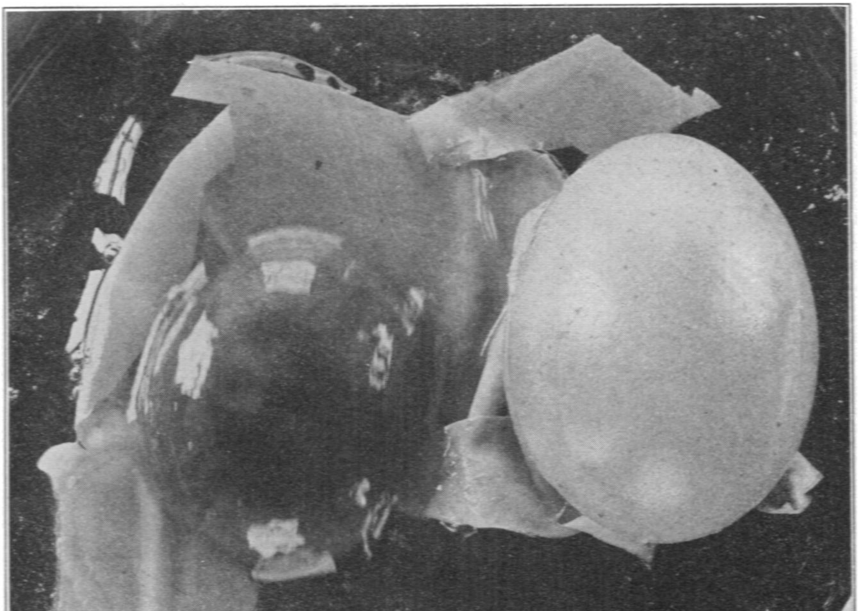

FIG. 2.

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PLATE III.

FIG. 1. Contents of dwarf egg No. 3. Note normal yolk and hard-shelled dwarf egg which is enclosed only in the outer albumen layers of the normal egg.

FIG. 2. Photograph of the shells of both included and including egg of double egg No. 12.

FIG. 3. Photograph of eggs which were in separate egg membranes but which had been flattened against each other before the shell was deposited so that they were lightly held together by the thin layer of shell which was continuous over their exposed surfaces. Egg at the right was a normal egg. Egg at the left contained a normal yolk but there was no albumen present.

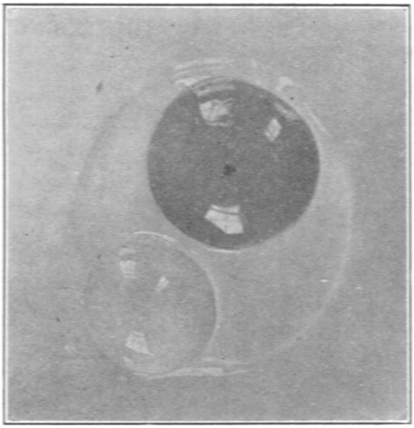

FIG. 1.

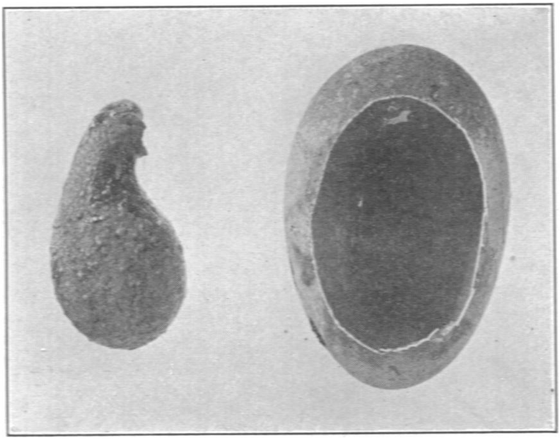

FIG. 2.

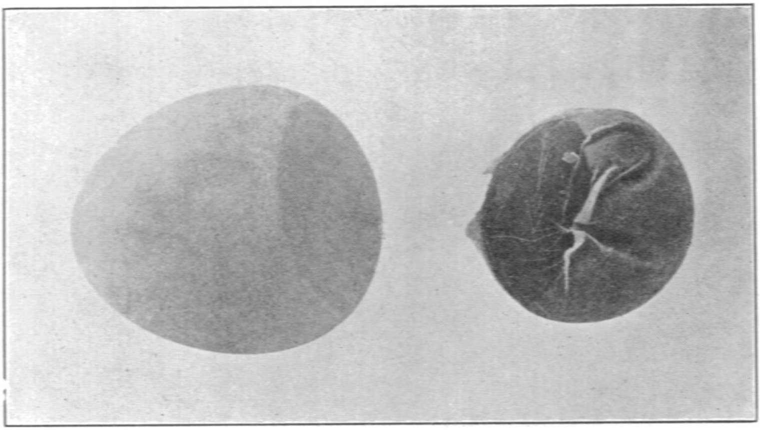

FIG. 3.

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